Monophyletic Origins of the Metazoa: An Evolutionary Link with Fungi

Patricia O. Wainright, Gregory Hinkle, Mitchell L. Sogin,* Shawn K. Stickel

A phylogenetic framework inferred from comparisons of small subunit ribosomal RNA sequences describes the evolutionary origin and early branching patterns of the kingdom Animalia. Maximum likelihood analyses show the animal lineage is monophyletic and includes choanoflagellates. Within the metazoan assemblage, the divergence of sponges is followed by the Ctenophora, the Cnidaria plus the placozoan *Trichoplax adhaerens*, and finally by an unresolved polychotomy of bilateral animal phyla. From these data, it was inferred that animals and fungi share a unique evolutionary history and that their last common ancestor was a flagellated protist similar to extant choanoflagellates.

Haeckel (*1*) first recognized that metazoans must share a common ancestry with a unicellular protist. In spite of numerous comparative studies and theories that link metazoans to flagellates (*1*) and ciliates (*2*), the origin of multicellular animals remains an open question. Morphology, ultrastructure, and complex embryological data do not provide support for any one hypothesis. The fossil record documents the Cambrian explosion of multicellular organisms (*3*) but provides few clues about protists ancestral to contemporary metazoa.

Comparisons of ribosomal RNA (rRNA) sequences have successfully established phylogenetic relations within the prokaryotic (*4*) and protist worlds (*5*), but similar procedures have given contradictory topologies for early diverging metazoan lineages (*6*). Distance and parsimony analyses of rRNA data portray protists as a series of independent branches that precede the nearly simultaneous separation of plants, animals, fungi, stramenopiles (chromophyte algae and heterokont protists), alveolates (ciliates, dinoflagellates, and apicomplexans) (*7*), and other independent protist lineages. Collectively, these abruptly diverging lineages define the crown (*8*) of the eukaryotic tree. Because nodes for each of the crown groups are separated by fewer than five nucleotide changes per thousand positions, their relative branching order has proven difficult to establish. The absence of early branching lines within each of the crown groups and inadequate representation of eukaryotic microbial diversity have compromised the utility of molecular data in resolving the origins of animals (*6*). In some studies, the reconstruction of organismal phylogeny is further exacerbated by incomplete sequence information (*9*) and inadequate methods for inferring molecular frameworks that include both slowly and rapidly evolving lineages (*6*).

We have reexamined relations between the animal kingdom and other major eukaryotic groups with the use of maximum likelihood methods (*10*) to analyze an expanded small subunit (16S-like) rRNA sequence database. Complete 16S-like rRNA sequences were determined for the choanoflagellates *Diaphanoeca grandis* Ellis, 1930 and *Acanthocoepsis unguiculata* Thomsen, 1973 and several lower metazoans, including the ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865; the cnidarian *Tripedalia cystophora* Conant, 1898; two porifera, *Microciona prolifera* (Ellis and Solander, 1786) and *Scypha lingua* Haeckel, 1872; and the placozoan *Trichoplax adhaerens* Schulze, 1883 (*11*).

Figure 1 is a maximum likelihood analysis (*12*) of 16S-like rRNA sequences from the groups that diverged at the crown of the eukaryotic tree. The fraction of 110 maximum likelihood bootstrap resamplings that support topological elements are shown above the branches (each resampling required 48 hours to compute). Values below the branches represent the fraction of 200 bootstrap neighbor-joining replicates (*13*) that support the evolutionary hypothesis in Fig. 1. In this phylogenetic framework, the metazoa comprise a monophyletic group that shares a most recent common ancestry with choanoflagellates. The animal and fungal lineages share a more recent common ancestor than either does with the plant, alveolate, or stramenopile lineages. Within the metazoan subtree, the sponge and ctenophore lineages diverge first, followed by placozoa and cnidarians, and then by a poorly resolved polychotomy leading to triploblast animal phyla. Although the

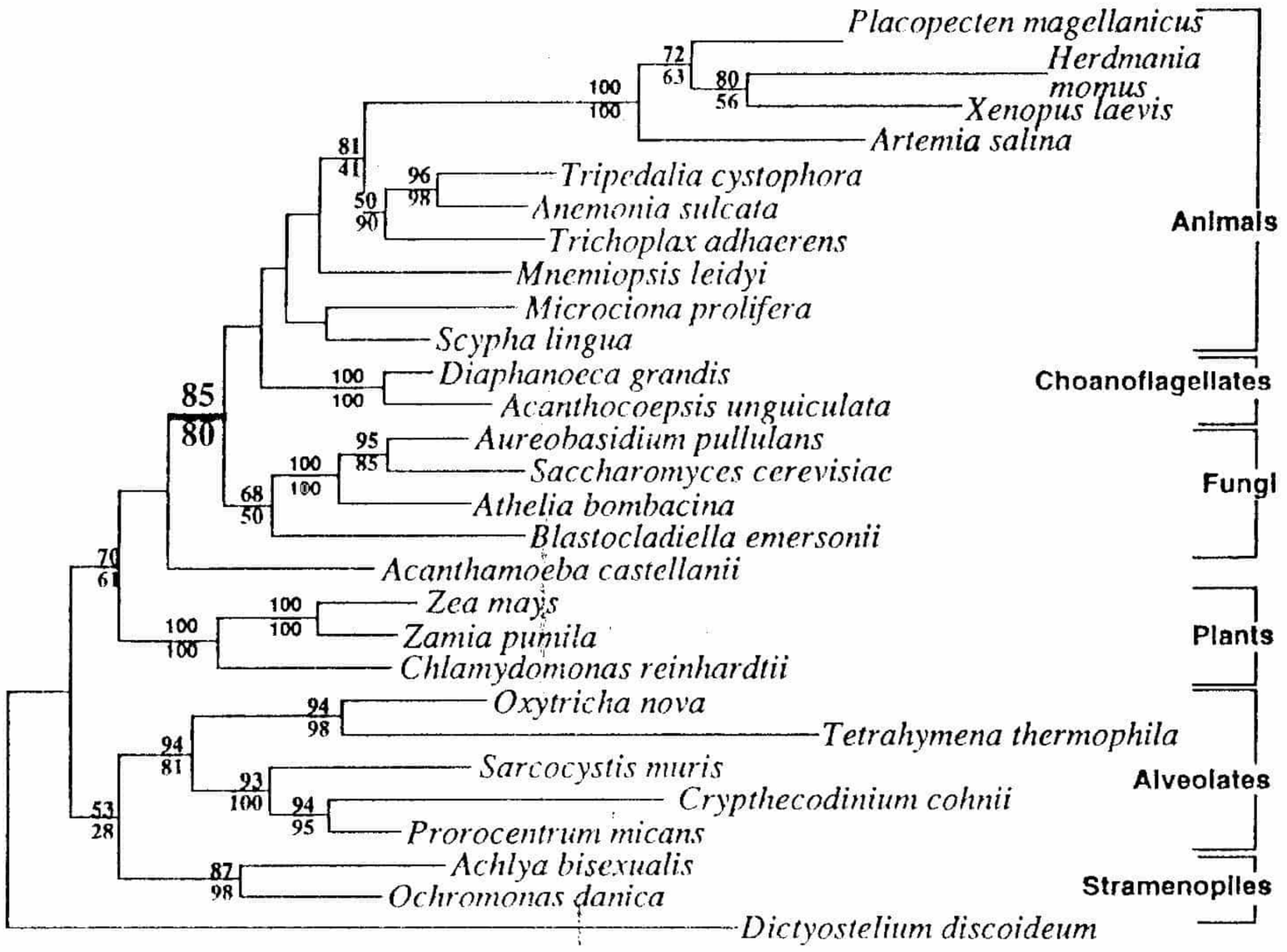

Fig. 1. Relation between animals, fungi, plants, and other eukaryotic groups inferred from complete 16S-like rRNAs. A computer-assisted method was used to align the 16S-like rRNA sequences from animals, plants, fungi, stramenopiles, alveolates, and other protist groups that diverged at the crown of the eukaryotic tree (*8*). Maximum likelihood methods (*10, 12*) were used to infer a molecular phylogeny with the use of sites that could be unambiguously aligned. The percentage of 110 bootstrap resamplings that support topological elements in maximum likelihood inferences is shown above the branches. The percentage of 200 neighbor-joining bootstrap replicates that corroborate topological elements in the figure is shown below the branches. The root of the tree is placed within the *Dictyostelium discoideum* lineage (*4, 5*). Confidence levels below 50% are not indicated.

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bootstrap values do not substantiate any single branching order for choanoflagellates, sponges, and ctenophores (*14*), the topology in Fig. 1 is consistent when alternative protist, fungal, and lower metazoan taxa are included in maximum likelihood analyses (*15*).

The early metazoan branching pattern confirms hypotheses about the relation of choanoflagellates and sponges to more complex animals (*16*). Haeckel (*1*) proposed that metazoans evolved from a colonial flagellate perhaps most similar to extant choanoflagellates. The cellular similarities between choanoflagellates and choanocytes of sponges are well known (*17*). Sponges can be loosely characterized as multicellular, and on a grade of relative complexity or organization lie between protists and metazoans (*18*). Multicellularity in the earliest diverging metazoans requires an extracellular matrix. In more complex animals, basement membranes provide structural support between epithelial and connective tissue (*19*). A central jellied matrix is found in the colonial choanoflagellate *Proterospongia haeckeli* (*20*), whereas in sponges more complex matrix components exist in the mesohyl (intercellular matrix) (*21*). Furthermore, basement membrane–like structures have been observed in sponges (*22*).

On the basis of gross morphology, ctenophores and cnidarians were at one time grouped in the phylum Coelenterata (*23*). Their deep divergence in our rRNA phylogeny is more consistent with the placement of ctenophores and cnidarians in separate phyla in accordance with differences in adult morphology and patterns of development (*24*). Our maximum likelihood analysis shows moderate bootstrap support for an earlier divergence of ctenophores relative to the separation of triploblastic animals from cnidarians and placozoans. Nonmolecular evidence in support of this branching pattern is equivocal. Ctenophores have mesenchymal muscle cells, gonoducts, and determinate embryological cleavage patterns (*25*), all characteristic of triploblastic animals. However, cell junctions that facilitate intercellular support and communication (*26*) are similar in sponges and ctenophores. Homologous structures are more highly developed in cnidarians (*27*). Finally, if the branching pattern in Fig. 1 accurately represents the evolutionary history of early diverging metazoan lineages, a loss of specialized intercellular structures in placozoans must have occurred (*28*).

The most important conclusion from our maximum likelihood analysis is the specific phylogenetic relation between animals and fungi. The fungi and animals represented in our data set are also united in maximum parsimony, least squares distance matrix, and neighbor-joining analyses (*29*). Independent confirmation of a conjoint evolutionary history for animals and fungi is provided by maximum likelihood analyses of amino acid sequences for elongation factors (*30*). At different times, fungi have been considered to be plants, members of other protist groups, or, in more contemporary schemes, worthy of kingdom level status (*31*). Molecular phylogenies based on 16S-like rRNA sequence comparisons (*32*) describe the higher fungi as a monophyletic group with flagellated chytrids representing the earliest diverging lineage. Most conventional phylogenies place the origin of Metazoa among protists, but Towe (*33*) and more recently Cavalier-Smith (*34*) argue that similarities in complex biosynthetic pathways, including syntheses of hydroxyproline, chitin, cellulose, and even ferritin, suggest a specific evolutionary relation between fungi and animals. Because chytrids and choanoflagellates both have flattened mitochondrial cristae and a single posterior flagellum, the hypothetical protist that represents the most recent common ancestor to the animals and fungi in the rRNA phylogeny very likely was a unicellular protist with these ultrastructural characteristics. This new rRNA phylogeny that recognizes the origins of animals and their relation to fungi provides a framework and a rational basis through which the origins and diversifications of metazoan phenotypes may be explored.

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12. The fastDNAml program written by G. Olsen (G. Olsen, M. Matsuda, R. Hagstrom, R. Overbeek, in preparation) is derived from J. Felsenstein's version 3.4 DNAML (part of his PHYLIP package) and uses the generalized two-parameter model of evolution [H. Kishino and M. Hasegawa, *J. Mol. Evol.* 29, 170 (1989)]. Maximum likelihood trees were inferred from unambiguously aligned positions in the compared sequences. Using jumbled orders for taxa addition and allowing global swapping to cross three branches, we repeated the search for an optimal tree until the best log likelihood score (ln likelihood = −16987.92530 for the tree in Fig. 1) was reached in at least three independent searches. The average computation time for 28 taxa with a SUN SPARC2 workstation was 48 hours.
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structed with single choanoflagellate, sponge, and cnidarian representatives. In all cases, the best tree topologies as judged by optimal log likelihood scores displayed branching patterns that were consistent with the phylogeny in Fig. 1.
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RANDOM SAMPLES

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Hyperactivity Tied to Gene Defect

Scientists at the National Institutes of Health say they have, for the first time, found an association between a specific genetic defect and a behavioral disorder. The disorder in question is ADHD, or attention deficit hyperactivity disorder, which afflicts about 5% of children and many adults as well. The culprit? In at least some cases, it's a gene coding for a defective thyroid hormone receptor that causes generalized resistance to thyroid hormone.

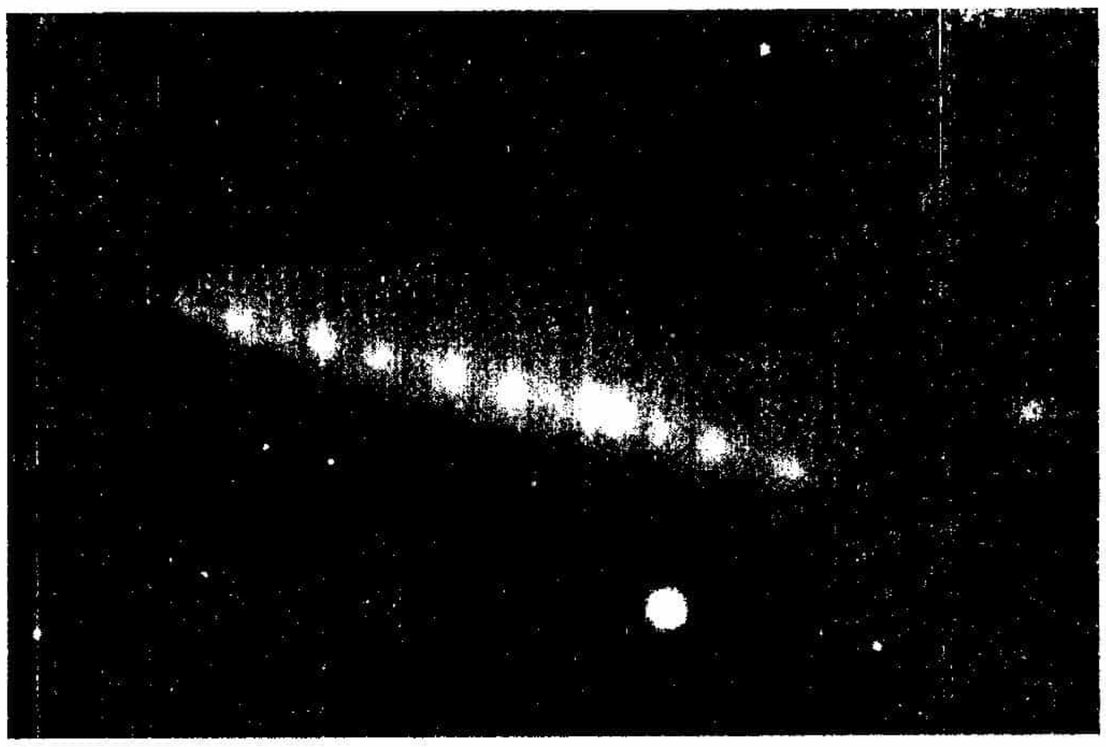
The news comes from a study, reported in the 8 April *New England Journal of Medicine*, that is based on a small and select population—104 adults and children belonging to 18 families, half of whose members have the defective gene. Among those with the defect, 70% were diagnosed with ADHD. Project director Bruce Weintraub of the National Institute of Diabetes and Digestive and Kidney Diseases says the nature of the connection has yet to be clarified, but that "thyroid hormone is essential to normal brain development."

While Weintraub says the defect probably accounts for no more than 5% of ADHD cases, he believes that the study opens the way for investigators to look for the roots of ADHD in other hormones as well as neurotransmitter receptor systems. The scientists do not rule out environmental causes for some cases of ADHD. But for the most part, says co-author Alan J. Zametkin of the National Institute of Mental Health: "It's not bad parenting, overcrowded schools, or unmotivated kids. ADHD is a neuropsychiatric problem based on brain physiology."

Wistar Settles With Koprowski

A year ago immunologist and vaccine pioneer Hilary Koprowski, now 78, sued Philadelphia's Wistar Institute contending that he had been removed as the institute's director only because of his age. Last week Wistar announced that an out-of-court settlement has been reached. A Wistar press-release says the terms of the settlement are confidential but that the institute is happy to "heal the relationship" with Koprowski.

Koprowski is happy too, according to one of his Philadelphia attorneys, Hugh J. Bracken. Bracken says Koprowski will promptly be made a member of the Wistar board of directors, that he will continue his research there, and that there are also "financial aspects" to the settlement.



JANE LUU AND DAVID JEWITT

Cometary pearls aglow. A comet's disruption produced at least 17 pieces, 10 of which can be seen in this false-color reproduction—suggesting that comets are indeed piles of rubble.

Did Jupiter Make a Comet Go to Pieces?

Comets take their bows as fuzzy balls of light—usually. But on the night of 24 March, Carolyn Shoemaker, one of history's premier comet finders, along with her husband, Eugene Shoemaker of the U.S. Geological Survey in Flagstaff, and noted amateur comet hunter David Levy of Tucson, found themselves looking at a most peculiar comet image from an 18-inch survey telescope on Mt. Palomar: A body was registering as a broad band of light.

Word of the find, dubbed Comet Shoemaker-Levy, flashed around the world, courtesy of the astronomers' alert network. Comets had been seen in as many as five pieces, but 2 nights later James Scotti and David Rabinowitz of the University of Arizona, observing at Kitt Peak, resolved the long blur into a string of first five and then 11 individual bodies. Next came Jane Luu of the University of California, Berkeley, and David Jewitt of the University of Hawaii, using the 88-inch telescope on Mauna Kea. They detected 17 fragments. Everyone agreed that this was a comet like no other. So what had broken Shoemaker-Levy into a train of what look like glowing embers?

No one is sure yet, but Brian Marsden of the Harvard-Smithsonian Center for Astrophysics suspects the culprit was Jupiter. Backtracking along the cometary trajectory, he found that Shoemaker-Levy had swept by the giant planet last summer, possibly so close that Jupiter's gravity tore apart the chunk of ice, rocky dust, and organic goo. That would jibe with an idea put forth in recent years that comets are "rubble piles" that only loosely agglomerated when they came together at the formation of the solar system.

Marsden figures that the sun's heat will drive off the ice of the smaller pieces and thus end their brief careers. In fact, all the debris from Shoemaker-Levy may disappear from sight, says Marsden. Whatever its fate, though, the comet will not threaten Earth—its orbit brings it no closer than Jupiter.

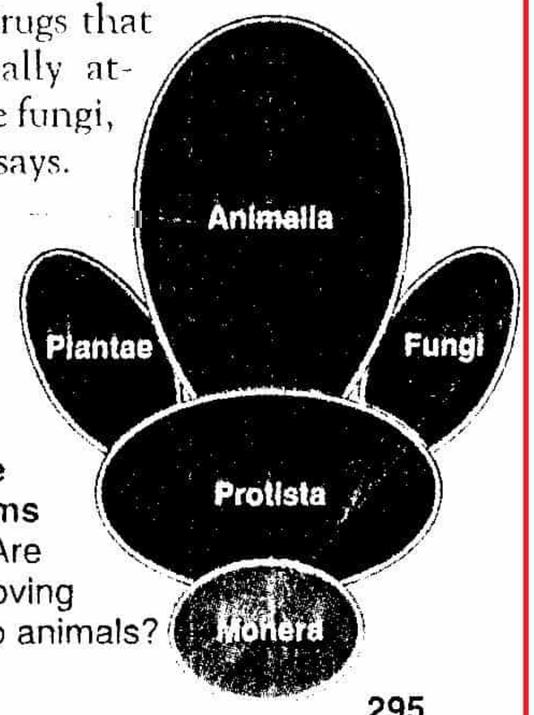
A Fungus on Our Family Tree

What's the most distant living thing from a human being you can imagine? Does a virus come to mind? How about a fungus? If that's your answer, you're barking up the wrong tree—according to a paper published in this issue of *Science* (see page 340).

It's generally been assumed that fungi, one of the five kingdoms of life, are more closely related to plants than they are to animals. But now Mitchell Sogin, a molecular evolutionist at the Marine Biological Laboratory in Woods Hole, has found evidence that fungi share a common ancestor with members of the animal kingdom.

After analyzing sequences of ribosomal RNA, Sogin's team found that the ancestor in question appears to be an ancient one-celled creature similar to choanoflagellates, a kind of protist. Sogin's work adds a certain yeastiness to a speculation, aired a decade ago by Smithsonian Institution biochemist Kenneth Towe, that the similar biosynthetic pathways of animals and fungi might make them cousins—at least distant ones. "Sogin's work is beautiful to me, it supports what I saw as an off-the-wall suggestion," Towe says.

Sogin's research has generated an infectious enthusiasm among his colleagues. The close ancestry between animals and fungi "may explain why fungal pathogens are so hard to control," says Berkeley mycologist John Taylor. The reason: Antifungal drugs target a complex biochemical cascade also found in humans. The similarities make it hard to develop drugs that specifically attack the fungi, Taylor says.



The five kingdoms of life. Are fungi moving closer to animals?